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Use of anthropogenic material affects bird nest arthropod community structure: influence of urbanisation, and consequences for ectoparasites and fledging success

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Abstract Nests are a critically important factor in determining the breeding success of many species of birds. Nevertheless, we have surprisingly little understanding of how the local environment helps determine the materials used in nest construction, how this differs among related species using similar nest sites, or if materials used directly or indirectly influence the numbers of offspring successfully reared. We also have little understanding of any potential links between nest construction and the assemblage of invertebrates which inhabit nests, in particular, ectoparasites. We addressed these questions by monitoring the success rates of Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major*, using nest boxes in rural, urban greenspace and urban garden settings. We collected used nests, identified the arthropods present, and measured the proportions of highly processed anthropogenic materials used in nest construction. Twenty-five percent of Great Tit nest materials were of anthropogenic origin and this was consistent across habitats, while Blue Tits used little (1–2%) anthropogenic material except in gardens (~16%), suggesting that Great Tits preferentially sought out these materials. In fledged nests, an increasing use of anthropogenic material was associated with a lower general arthropod diversity and ectoparasite predator abundance (Blue Tits only), but higher levels of Siphonaptera (fleas).

Higher arthropod diversity was associated with lower flea numbers, suggesting that increased diversity played a role in limiting flea numbers. No direct link was found between breeding success and either anthropogenic material usage or arthropod diversity and abundance. However, breeding success declined with increasing urbanisation in both species and increased with nest weight in Blue Tits. The interplay between urbanisation and bird ecology is complex; our work shows that subtle anthropogenic influences may have indirect and unexpected consequences for urban birds.

Keywords Blue Tit · Great Tit · Nest boxes · Human–wildlife interactions · Urban ecology

Zusammenfassung

Die Verwendung anthropogener Baumaterialien beeinflusst die Struktur der Arthropodengemeinschaften in Vogelnestern: Auswirkungen der Verstädterung und die Folgen für Ektoparasiten und Ausfliegerfolg

Für den Bruterfolg vieler Vogelarten stellen Nester einen Faktor von kritischer Bedeutung dar. Dennoch haben wir nur überraschend wenige Kenntnisse darüber, wie das lokale Umfeld zur Prägung des verwendeten Baumaterials beiträgt, wie sich diesbezüglich verwandte Arten unterscheiden, welche ähnliche Nistplätze nutzen, oder ob die verwendeten Materialien direkt oder indirekt die Anzahl der erfolgreich aufgezogenen Nachkommen beeinflussen. Auch wissen wir nur wenig über potenzielle Zusammenhänge zwischen der Nestbauweise und den Invertebratengesellschaften, speziell Ektoparasiten, welche die Nester besiedeln. Diesen Fragen gingen wir nach, indem wir die Erfolgsraten in Nistkästen brütender

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Blaumeisen *Cyanistes caeruleus* und Kohlmeisen *Parus major* aus ländlichen Bereichen, städtischen Grünflächen und aus Stadtgärten kontrollierten. Wir sammelten benutzte Nester, bestimmten die vorhandenen Arthropoden und maßen den Anteil der beim Bau verwendeten höher verarbeiteten anthropogenen Materialien. Etwa 25% des Nistmaterials bei Kohlmeisen stammte aus einer anthropogenen Quelle und zwar durchweg in allen Habitaten, während Blaumeisen nur wenig davon (1–2%) benutzten, außer in Gärten (~16%), was darauf hindeutet, dass Kohlmeisen diese Materialien bevorzugt sammelten. Bei benutzten Nestern hing die zunehmende Verwendung anthropogener Materialien mit einer geringeren allgemeinen Arthropodendiversität und Häufigkeit ektoparasitischer Prädatoren (nur bei Blaumeisen), jedoch größerer Mengen an Siphonapteren (Flöhen) zusammen. Eine höhere Arthropodendiversität stand mit geringeren Flohzahlen in Verbindung, was nahelegt, dass die höhere Diversität bei der Begrenzung der Flohzahlen eine Rolle spielt. Wir fanden weder einen direkten Zusammenhang zwischen Bruterfolg und der Verwendung anthropogener Materialien, noch zur Arthropodendiversität oder -häufigkeit. Allerdings nahm der Bruterfolg bei beiden Arten mit zunehmender Verstädterung ab und nahm bei den Blaumeisen mit dem Nestgewicht zu. Das Zusammenspiel zwischen Urbanisierung und der Ökologie der Vögel ist komplex; unsere Arbeit zeigt, dass geringfügige anthropogene Einflüsse indirekte und unerwartete Folgen für Vogelarten in Siedlung haben können.

Introduction

Today, over half of the world's human population lives in ever-growing towns and cities [United Nations (UN) 2011], which are increasingly recognised as being of considerable value for bird diversity and abundance (Gregory and Baillie 1998; Davies et al. 2009; Evans et al. 2011; Aronson et al. 2014). The changes in habitat and resource availability associated with urbanisation have a marked effect on the life histories of urban birds (Chace and Walsh 2006). Urban-dwelling birds tend to lay eggs earlier, produce smaller clutches and lighter nestlings, and have lower average productivity per nesting attempt than their non-urban conspecifics (Chamberlain et al. 2009). The lower availability of natural foods in urbanised areas results in lower food provisioning to nestlings, and while supplementary feeding can be ubiquitous in urban areas (Davies et al. 2009; Orros and Fellowes 2015a; Hanmer et al., in review), the benefits for bird productivity are not clear (Robb et al. 2008; Harrison et al. 2010; Plummer et al. 2013).

Many wild bird species utilise a diversity of urban habitats, and private suburban gardens are particularly important in this context (Cannon et al. 2005; Chamberlain et al. 2005). Aside from the provision of supplementary food, other resources provided by people help support some urban bird populations. In the UK it is estimated that more than one in five gardens contains a bird nest box, equating to a minimum of 4.7 million nest boxes, nationally equivalent to the provision of one nest box for every six breeding pairs of cavity-nesting birds (Davies et al. 2009). The availability of suitable nesting sites limits breeding density (Newton 1998) and with the removal of mature and dead trees typical of suburbia, there will be fewer natural nest sites in such areas (Wiebe 2011). Buildings may provide some cavities, but modern or refurbished houses tend to have fewer potential nesting holes to compensate for this loss of nesting sites (Mason 2006; Shaw et al. 2008). As a result, the provision of nest boxes in urban areas may be a particularly valuable resource, allowing cavity nesters to prosper (Chace and Walsh 2006; Wiebe 2011) and providing an opportunity to investigate factors affecting urban bird breeding biology.

Despite the potential importance of nest site provisioning and the influence of urbanisation on wild bird populations, our understanding of the effect of urbanisation on bird nesting biology remains relatively limited (reviewed in Deeming and Reynolds 2015). Factors that potentially affect breeding success are of considerable interest, and species that utilise nest boxes offer a practical way to explore these effects (Crocì et al. 2008). There are several possible ways that urbanisation can influence bird nests. There is evidence for geographic variation within species in nest construction, with nests constructed in cooler regions typically being larger and better insulated (Deeming et al. 2012; Mainwaring et al. 2014; Biddle et al. 2016). Due to the urban heat island (UHI) effect increasing local environmental temperatures, it is plausible that nests from more highly urbanised areas may need less insulation, leading to smaller, lighter nests requiring less energy investment to build. However, there is little if any evidence that a change of the magnitude associated with the UHI effect influences bird reproduction (Deviche and Davies 2014).

Increased urbanisation may also be associated with a change in the proportion of anthropogenic material incorporated into nests (Reynolds et al. 2016). Given the general decline in biodiversity seen with increasing urbanisation (McKinney 2008), the availability of some key natural nesting materials may diminish, while the availability of potentially suitable anthropogenic alternatives is likely to increase. Depending on behavioural preferences and nest location this may cause some birds to expend more energy finding suitable natural nesting material, or instead they

may utilise whatever is readily available (Britt and Deeming 2011), and so with higher levels of urbanisation incorporate more anthropogenic material into their nests (Wang et al. 2009; Reynolds et al. 2016). Given the potentially high insulation value of some anthropogenic materials they may be preferred and such preferences (if any) may differ between species (Surgey et al. 2012; Suárez-Rodríguez et al. 2013). Anthropogenic material incorporated into nests may also be hazardous to bird survival and breeding success, particularly by causing entanglement (Votier et al. 2011; Townsend and Barker 2014), but possibly also through more subtle effects on bird health. For example, House Sparrows *Passer domesticus* incorporating discarded cigarette butts into their nests reduce their ectoparasite load at the cost of exposure to toxins (Suárez-Rodríguez et al. 2017). For the purposes of this study we define anthropogenic material as highly processed anthropogenic material (e.g. polyester, nylon, highly processed cotton), although we acknowledge that hair from domestic animals and material from exotic garden plants could be considered to be anthropogenic in origin.

Changes in nest construction may in turn influence the invertebrate assemblage present in nests, of which changes in the presence and abundance of bird ectoparasites is of primary interest in this context. The influence of nest construction on ectoparasite load has been explored in a number of studies (e.g. Moreno et al. 2009; Suárez-Rodríguez et al. 2013) but only one has previously been carried out in a European urban environment (Reynolds et al. 2016), focusing on fleas and Blue Tits. Generalist nest-dwelling ectoparasites such as fleas (Siphonaptera) and biting mites (Acari, principally the family Dermanysidae) are common in passerine nests (Moreno et al. 2009; Cantarero et al. 2013), but the latter are rarely considered.

Ectoparasites may influence reproductive success in a number of ways, such as by reducing nestling growth and survival (Merino and Potti 1995) or by affecting adult health (Tomás et al. 2007), possibly leading to nest desertion (Oppliger et al. 1994). Nest composition may influence ectoparasite load by affecting larval mortality and growth through effects on nest humidity (Heeb et al. 2000) or through the attraction/repellence effects of the materials themselves (Remeš and Krist 2005; Mennerat et al. 2009a; Tomás et al. 2012). As nest construction and host defence behaviour may differ significantly between species utilising similar nest sites in a local area, ectoparasite loads may also differ (Moreno et al. 2009).

Bird nests are also potentially home to a diverse array of non-parasitic arthropods (Tryjanowski et al. 2001). To our knowledge, no studies have considered the influence of nest construction on this diversity in the context of urbanisation. In turn, it is unclear what (if any) effect these arthropods have directly or indirectly on the breeding

success of birds. Notably, Křištofík et al. (2017) found that adding saprophagous larvae of *Fannia* sp. to nests containing young European Bee-eaters *Merops apiaster* increased nestling condition, as the larvae consumed nest and nestling waste and detritus and so improved conditions in the nest cavity. While unstudied, some invertebrates may also predate other nest-dwelling invertebrates, including ectoparasites, depressing their numbers and thus potentially increasing bird productivity. Just how urbanisation affects the diversity of nest-dwelling invertebrates is not understood; it is possible that their diversity will decline with increasing urbanisation, as more generally found with invertebrates (McKinney 2008; Jones and Leather 2012). Irrespective of this relationship, we hypothesise that increased diversity in the nest may be associated with increased nesting success.

Taken together, it is evident that nest material could influence breeding productivity, and may also influence ectoparasite load. What is not clear is if there is a consistent influence of urbanisation on these factors, if species show similar responses, or if the wider nest arthropod community also varies with urbanisation. To examine this we compared (1) nesting materials, (2) ectoparasite load, (3) the assemblage of other arthropods and (4) fledging success, of two common British urban 'adapter' passerine species, the Blue Tit and Great Tit, at different levels of urbanisation in and around a large urban area.

Methods

Study areas

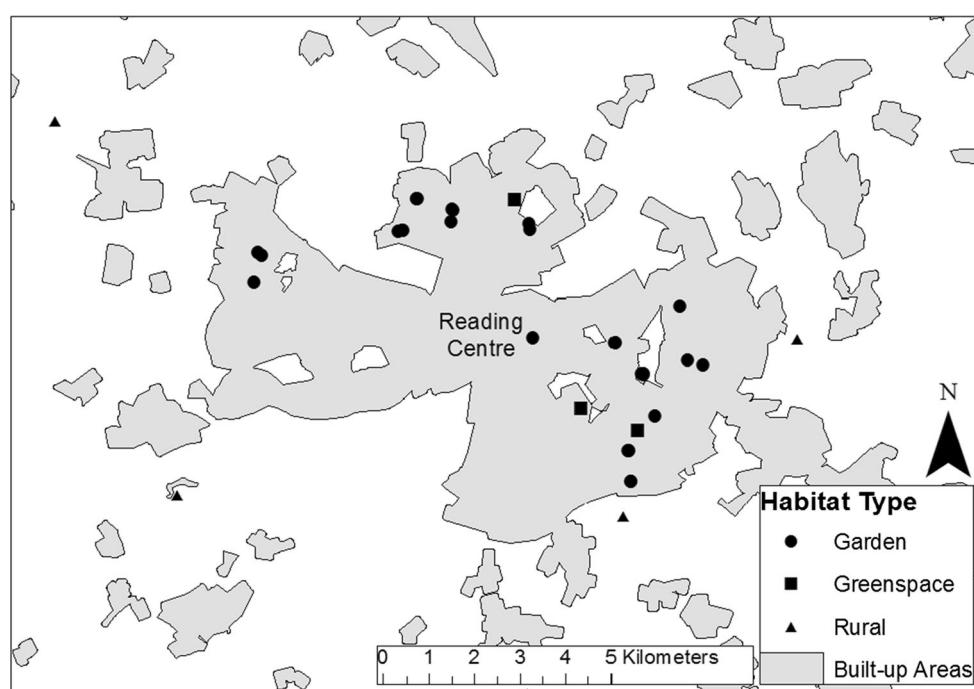
This study was conducted in and around the large urban district centred on Reading, South East England, between April and June 2016. Greater Reading covers approximately 72 km² and has a population of ~290 000 people (Office for National Statistics 2013; following Orros and Fellowes 2015a).

Volunteer garden owners were recruited across Reading through other studies previously run by the People and Wildlife Research Group, leafleting and word of mouth. Additional nest boxes were monitored on the grounds of the University of Reading, the Hill Primary School and Beale Wildlife Park and Gardens in addition to Maiden Erlegh Lake, Lavell's Lake and Hosehill Lake local nature reserves (Fig. 1).

Nest monitoring

Nest boxes were monitored from early April until final fledging in late June. Only one breeding attempt per nest box was monitored and all boxes were cleared of old

Fig. 1 The distribution of study sites in and around the Greater Reading area indicated according to broadly defined habitat types



nesting material prior to the breeding season. Approximately 350 potentially useable nest boxes were monitored for this study. Once a nesting attempt was found it was checked up to twice a week until fledging or confirmed failure following the British Trust for Ornithology (BTO) Nest Record Scheme (<https://www.bto.org/volunteer-surveys/nrs>). All surviving chicks were ringed at approximately 14 days old under BTO ringing permit C5258. Dead chicks were removed whenever found during monitoring. All nest boxes were measured to establish their internal dimensions and their locations plotted using a global positioning system (GPSMAP 60CSx; Garmin, USA). Within sites, boxes were of effectively the same design and size but there was some variation between sites which was controlled for in the mixed-models analysis by the inclusion of site as a random factor.

Nest materials and arthropod load

Successful nests were removed between 2 days and 3 weeks from the estimated fledging date and sealed in plastic bags (Moreno et al. 2009). Failed nests that had grown chicks were removed when all the chicks were found to have died or had been predated. Nests that failed at the egg stage were removed when they had apparently been abandoned for at least a month beyond the estimated hatch date and there was no evidence of adult attendance. Fully predated nests were removed when they were found, provided significant damage had not been done to the nest that had lead to the removal of material. All remaining

unhatched eggs and dead chicks were disposed of during nest removal. Nests were removed during the breeding season under Natural England license 2016-23468-SCI-SCI (granted to H. J. H.). All bagged nests were stored in a cold room at ca. 5 °C for up to 4 weeks. They were then placed in Tullgren funnels equipped with 60-W bulbs to extract invertebrates. Nests were dried for 48 h then weighed to the nearest 0.01 g on an electric balance. Nest materials were then broken down into apparently natural material from the environment (plant matter and natural fibres such as animal hair) and processed anthropogenic material (primarily dyed, treated cotton and artificial materials); each element was weighed separately.

Extracted invertebrate samples from each nest were collected and stored in tubes containing 40 ml of 70% ethanol solution. Due to variation in collection time in failed and some fledged nests, invertebrate data were only collected from the successful nests removed within 3 weeks of fledging. Arthropods were sorted under a dissecting microscope (maximum magnification 100×; Nikon SMZ645; Nikon, Japan) to order and subsequently identified to lower taxonomic levels where practical, particularly in the case of likely ectoparasites. All arthropods were individually counted, with the exception of flea larvae where numbers were on rare occasions very large. In the latter situation a subsample of 25% of the material was counted, and total numbers of larvae then extrapolated from these data. Shannon diversity indices at the order level were calculated for each fledged nest examined for arthropods.

Habitat data for each collected nest were established for a 200-m radius around each nest box in ArcGIS 10.0 (ESRI 2011) using data from the Ordnance Survey Mastermap collection (EDINA, University of Edinburgh) land use data. Habitat/land use categories within 200 m of collected nests were grouped together to form four broad categories: constructed surfaces (buildings, roads, driveways and pavements); natural surfaces (trees, scrub and grassland); water bodies (primarily lakes and ponds); and private gardens (defined as garden mixed surfaces).

Analysis

All analyses were carried out within program R, version 3.3 (R Core Team 2016). Mann–Whitney *U*-tests were used to compare between bird species and within species between broad habitat types (garden, greenspace and rural) for productivity and nest construction. Spearman's rank correlation was used to examine the relationship between percentage habitat cover and nest construction across all collected nests. For the subset of fledged nests collected under a standardised methodology and fully examined for arthropods, Mann–Whitney *U*-tests were carried out to compare between species overall and within species between broad site types for ectoparasite abundance, a measure of arthropod predator abundance (total numbers of Pseudoscorpionida, Staphylinidae and Histeridae) and arthropod diversity. For all multiple comparisons, *p* was automatically corrected for the false discovery rate within R.

Separate mixed-effects models for Blue Tits and Great Tits were carried out using R package lme4 (version 1.1-12; Bates et al. 2015) to examine effects of nest construction and habitat separately on the proportional usage of anthropogenic material and overall nest fate (both binomial models) along with the number of eggs laid and number of chicks fledged in failed and successful nests (both Poisson models). Predated nests were excluded from models examining nest fate and the number of chicks fledged to control for the influence of direct nest predation on breeding success (Lambrechts et al. 2016a). Separate additional mixed-effect models were run for the subset of nests examined for arthropod diversity and ectoparasite load. These examined Shannon diversity (linear model), overall flea abundance (Poisson model) and the presence/absence of Dermanyssidae mites (binomial model). To explore influences of these factors along with nest construction and habitat, the final models considered all potential factors influencing number of eggs laid and chicks fledged just for these nests.

In all mixed-effect models, individual study site (rather than broad site type) was treated as a random effect to account for the potential non-independence of nests from

the same site and for the slight variation in box design between sites. In overdispersed models, individual nest identity was added as an additional random effect (Harrison 2014). Nest boxes within 200 m of each other, or on the same property/reserve, were considered to be from the same site. Model selection was carried out on the global models using delta Akaike information criteria (ΔAICc) and model weights (Burnham and Anderson 2002). From the models within $\Delta 2 \text{ AICc}$ of the minimal model, predicted lines of best fit with 95% confidence intervals were calculated for plotting. With the exception of Shannon diversity models, the proportion of constructed surfaces was used as a measure of urbanisation. In the Shannon models the total proportion of green surfaces (natural surfaces and gardens) was found to produce more stable models and so was utilised instead, whereas the reverse was true for models considering all other dependent variables. For models considering the number of chicks fledged, clutch size was used as a fixed factor to account for any relationship between the two.

Results

Overall nests

In total 98 nests (62 Blue Tit and 36 Great Tit) were fully monitored and deconstructed. Of these at least one chick apparently fledged in 60 (35 and 25, respectively) nests, while in the other 38 (27 and 11, respectively) nests, the egg or chick stage failed. Five Blue Tit and one Great Tit nest seemingly failed due to direct predation. Breeding and nest construction parameters for collected nests at different levels of urbanisation are summarised in Table 1.

Nest composition

With Blue Tits rural nests were significantly heavier than urban greenspace nests ($W = 368$, $p = 0.04$, other comparisons $p > 0.1$; Table 1) while Great Tit nests showed no significant differences between habitat types (all $p > 0.1$; Table 1). There was no significant difference in nest box size (using interior base surface area) between broad habitat types in either species (both $p > 0.1$; Table 1).

Nest materials included mosses, grasses, leaves, twigs, feathers, animal hair (both domestic and wild) and anthropogenic materials, which were largely treated cotton and artificial stuffing materials. Anthropogenic material was found in 77 and 94% of Blue Tit and Great Tit nests, respectively (84% of all nests). Blue Tit nests contained proportionally less anthropogenic material and showed considerably more variation in rates of use than Great Tit nests ($W = 590.5$, $p = 0.001$; Table 1). There was no

Table 1 Summary of productivity parameters and nest construction for collected Blue Tit and Great Tit nests in the study

Species	Habitat	Overall success rate	Eggs laid	Chicks fledged	Proportion anthropogenic material	Nest dry weight (g)	Nest box base surface area (cm ²)	<i>n</i> nests (sites)
Blue Tit	Rural	0.79	8.0 (7.0–8.5)	4.0 (2.0–6.0)	0.02 (0.00–0.08)	25.1 (22.9–27.1)	150 (149–221)	29 (4)
	Greenspace	0.42	8.0 (6.5–9.0)	0.0 (0.0–4.0)	0.01 (0.00–0.14)	20.2 (17.2–24.5)	150 (144–180)	27 (4)
	Garden	0.53	8.0 (7.0–8.3)	0.5 (0.0–2.3)	0.16 (0.01–0.25)	22.4 (18.9–25.7)	161 (128–190)	16 (15)
	Overall	0.56	8.0 (7.0–9.0)	2.0 (0.0–4.8)	0.02 (0.00–0.16)	22.7 (18.3–25.9)	150 (144–192)	62 (23)
Great Tit	Rural	1.00	7.0 (6.0–7.0)	5.0 (4.0–5.0)	0.23 (0.17–0.33)	30.4 (24.5–38.8)	221 (150–221)	9 (5)
	Greenspace	0.67	6.0 (4.0–6.0)	1.0 (0.0–3.0)	0.25 (0.05–0.31)	22.7 (17.3–31.7)	150 (150–192)	21 (4)
	Garden	0.44	6.5 (5.3–7.0)	0.5 (0.0–1.8)	0.25 (0.21–0.27)	27.0 (20.2–29.2)	166 (159–207)	6 (3)
	Overall	0.69	6.0 (5.0–7.0)	2.0 (0.0–4.0)	0.24 (0.12–0.32)	25.0 (18.7–34.0)	157 (150–192)	36 (12)

Median values with interquartile ranges (IQR; *in parentheses*) are included to summarise variation in the data where appropriate

effect of habitat type on the use of anthropogenic materials for either species ($p > 0.09$ for all comparisons). In a logistic mixed-model regression controlling for site, neither species showed a significant association between either broad habitat type or the actual level of urbanisation as a proportion of constructed surfaces and the proportion of anthropogenic materials used.

Nest arthropod diversity and ectoparasite load

Due to the more standardised collection of nests and the loss of several invertebrate samples, only 42 fledged nests (23 Blue Tit and 19 Great Tit) from 15 different sites were explored for their arthropod diversity and numbers. Arthropods from 19 different orders were found in nests (Table 2). Parasitic Dermanyssidae mites were found in 55% of nests, so this data was treated as presence/absence data. Adult Siphonaptera (fleas) or their larvae were found in all but one nest. All adults were identified as members of the *Ceratophyllus* and were most likely Hen Fleas *Ceratophyllus gallinae* (Harper et al. 1992), with the exception of one individual *Dasypsyllus gallinulae*. As they are functionally alike and flea larvae could not readily be separated to species, and a number of nests contained high numbers of larvae but no adults, all fleas were combined together into a single category to form an overall measure of flea abundance in nests. Mallophaga (biting/bird lice) and Analgoidea (feather mites) were only found in single nests and so were not included in the ectoparasite analysis. Amongst the other arthropods found, potential predators of mites or fleas were identified in 52% of nests (adult predators only). Staphylinidae (Rove Beetles) were the most frequently recorded coleopterans, and these prey on other insects and mites. Other potential predators included Histeridae beetles, Pseudoscorpions (Pseudoscorpiones) and some predatory mites of the suborder Prostigmata (Table 2).

There was no difference in Shannon diversity at the order level between fledged Blue Tit and Great Tit nests ($H_s = 1.29$ and $H_s = 1.28$, respectively) and within species no significant difference between the broad site types ($p > 0.1$ in all cases; Table 3). For Blue Tit nests, the AICc-selected logistic regression mixed-effect model for factors influencing Shannon diversity found that the proportion of green surfaces within 200 m (used instead of constructed surfaces due to poor model stability) were positively associated with increased diversity [$\chi^2(1) = 5.34$, $p = 0.024$, following Bates et al. 2015; Fig. 2; Table 4]. No effect was found for Great Tits.

There was no significant difference between the overall abundance of fleas or Dermanyssidae mites in nests between bird species, or within species across habitat types ($p > 0.1$ in all cases; Table 3). Fleas showed a significant negative correlation with Shannon diversity overall and specifically in Blue Tits ($r_s = -0.37$, $p = 0.016$ and $r_s = -0.42$, $p = 0.048$, respectively). No significant correlation was found in the Dermanyssidae and there was no correlation between the abundance of mites and fleas.

An increase in potential predator abundance (total Pseudoscorpionida, Staphylinidae and Histeridae) was associated with a decrease in the proportion of anthropogenic nest material in the Blue Tit nests ($r_s = -0.52$, $p = 0.012$; Fig. 3). There was a high outlier in the predator numbers and the correlation was still highly significant following its removal ($r_s = -0.55$, $p = 0.008$; see Fig. 3). Predator abundance or presence/absence was not significantly associated with or affected by any other variables including ectoparasite abundance (all $p > 0.09$). No relationship was found between predator abundance or presence/absence and any other measured variable in Great Tits ($p > 0.1$).

In Blue Tits the minimal model for flea abundance could not be distinguished from the null model ($\Delta\text{AICc} < 2$). In

Table 2 All arthropods detected in Blue Tit and Great Tit nests identified to at least order with summary statistics for both Blue Tits and Great Tits

Class	Order	Total numbers in Blue Tit nests (median; IQR)	Total numbers in Great Tit nests (median; IQR)	Identified families	Notes
Arachnida-subclass Acari (mites)	Oribatida	42 (0; 0–1)	11 (0; 0–1)		
	Trombidiformes (suborder Prostigmata)	800 (0; 0–1)	7 (0; 0–0)	Tetranychidae (Spider Mites) Cheyletidae?	Some predators Some predators and Ectoparasites
	Mesostigmata	1103 (14; 2.5–43.5)	1435 (38; 4–82)	Dermanyssidae (biting mites) Laelapidae	Ectoparasites
	Sarcoptiformes	2593 (47; 3–130.5)	4597 (21; 0.5–72)	Acaridae Analgoidea (Feather Mites) Glycyphagidae	Ectoparasites
Other Arachnida	Araneae (spiders)	4 (0; 0–0)	9 (0; 0–0.5)		
	Pseudoscorpionida (pseudoscorpions)	3 (0; 0–0)	0		Potential ectoparasite predators
Malacostraca	Isopoda (woodlice)	21 (0; 0–0)	14 (0; 0–0)		
Collembola (springtails)	Entomobryomorpha	80 (0; 0–3.5)	37 (2; 0–2.5)	Entomobryoidea	
	Poduromorpha	2 (0; 0–0)	0	Poduroidea	
Insecta (insects)	Coleoptera (beetles)	325 (0; 0–15.5)	670 (1; 0–7.5)	Staphylinidae (Rove Beetles) Latridiidae Corylophidae Histeridae (Clown Beetles)	Potential ectoparasite predators Potential ectoparasite predators
	Dermaptera (earwigs)	0	1 (0; 0–0)		
	Diptera (flies)	134 (0; 0–2)	216 (0; 0–1.5)	Psychodidae (Drain/Moth Flies)	
	Hymenoptera	7 (0; 0–0)	30 (0; 0–0)	Formicidae (ants)	
	Hemiptera (true bugs)	7 (0; 0–0)	1 (0; 0–0)	Aphidoidea (aphids) Aleyrodidae (White Fly)	
	Lepidoptera (moths)	530 (3; 1–10)	314 (7; 2–21)		
	Psocoptera (booklice)	62 (0; 0–0)	32 (0; 0–0)		
	Thysanoptera (thrips)	1 (0; 0–0)	0		
	Phthiraptera (lice) (suborder Mallophaga-bird lice)	3 (0; 0–0)	0		Ectoparasites
	Siphonaptera (fleas)	9110 (318; 46–611.5)	7531 (297; 159–515)	Ceratophyllidae	Ectoparasites: <i>Ceratophyllus gallinae</i> (Hen Flea) <i>Dasypsyllus gallinulae</i> (Moorhen Flea)

Families and notes on predatory/ectoparasites are included where known

Table 3 Summary of the arthropod Shannon diversity (H_s), ectoparasite load, productivity and nest construction for the subset of fledged nests examined for arthropod numbers and diversity

Species	Habitat	H_s	Fleas n	Nests with mites (%)	Eggs n	Chicks fledged n	Proportion anthropogenic material	Nest dry weight (g)	n nests (sites)
Blue Tit	Rural	0.76 (0.42–0.86)	442 (49–669)	43	7.0 (7.0–10.0)	5.0 (3.0–5.5)	0.10 (0.04–0.13)	21.2 (16.4–25.6)	7 (2)
	Greenspace	0.93 (0.70–1.23)	336 (67–626)	70	7.5 (7.0–8.0)	4.5 (4.0–5.8)	0.11 (0.00–0.23)	21.0 (19.0–25.0)	10 (4)
	Garden	1.09 (0.74–1.16)	135 (34–325)	50	7.5 (7.0–8.8)	2.5 (1.25–3.8)	0.07 (0.00–0.29)	17.6 (13.2–28.1)	6 (6)
	Overall	0.91 (0.65–1.15)	318.0 (46–612)	57	7.0 (7.0–9.0)	4.0 (3.0–5.0)	0.10 (0.01–0.17)	22.2 (18.1–26.2)	23 (12)
Great Tit	Rural	0.50 (0.40–0.60)	770 (657–883)	100	9.5 (7.0–12.0)	3.0 (2.0–4.0)	0.17 (0.02–0.32)	27.1 (24.5–29.7)	2 (1)
	Greenspace	0.86 (0.68–0.95)	297 (208–515)	55	5.0 (4.0–6.5)	3.0 (2.0–4.0)	0.30 (0.23–0.43)	19.3 (11.8–26.1)	11 (4)
	Garden	0.83 (0.67–1.09)	124 (30–265)	33	6.5 (6.0–7.0)	2.0 (2.0–3.5)	0.18 (0.04–0.22)	30.6 (26.2–36.3)	6 (6)
	Overall	0.84 (0.62–0.95)	297 (159–515)	53	6.0 (5.0–7.0)	3.0 (2.0–4.0)	0.29 (0.09–0.32)	24.5 (18.3–30.7)	19 (11)

All values are medians with IGRs (*in parentheses*) with the exception of nests with mites which show the proportion of those nests that contained Dermanyssidae mites, and rural Great Tit data which show the mean and IQR instead

Great Tits increasing levels of urbanisation (constructed surfaces) led to lower flea abundance, and another model within ΔAICc 2 additionally found a significant positive relationship between the proportion of anthropogenic material ($p = 0.001$ and $p = 0.052$, respectively; Fig. 4; Table 5). No model was found containing a significant predictor following selection for the presence of Dermanyssidae mites in the nests of either species. No relationship was found for either ectoparasite type with the weight of the nests, numbers of eggs laid or number of chicks fledged.

Influences on breeding success

Overall, Blue Tits laid significantly more eggs than Great Tits ($W = 1711.5$, $p < 0.001$; Table 1) per breeding attempt, but there was no overall difference in the number of chicks they fledged, nor in the proportion of nests that fledged at least one chick. In successful nests there was no significant correlation between the number of eggs laid and the number of chicks fledged in either species (both $p > 0.1$). The proportion of anthropogenic material was not a significant predictor of any measure of breeding performance.

There was no significant difference in the number of eggs laid in either species across sites, but rural breeding birds fledged significantly more chicks per breeding attempt than urban greenspace and garden breeding birds for both Blue Tits ($W = 368$, $p = 0.032$ and $W = 201.5$, $p = 0.028$, respectively; Table 1) and Great Tits ($W = 132$, $p = 0.001$ and $W = 39$, $p = 0.007$, respectively; Table 1). Increasing proportions of constructed surfaces as a measure of level of urbanisation did not significantly influence the number of eggs laid, but it did lead to fewer chicks being fledged in both species ($r_s = -0.32$, $p = 0.01$ and $r_s = -0.45$, $p = 0.006$ for Blue Tits and Great Tits, respectively).

For Blue Tits, an increased level of urbanisation was associated with reduced overall breeding success, ($p = 0.022$; Fig. 5). Heavier nests were associated with more eggs being laid ($p = 0.02$; Fig. 6a; Table 6) and more chicks fledged ($p = 0.008$; Fig. 6b; Table 6). Increased urbanisation also resulted in fewer chicks fledging ($p = 0.002$; Fig. 6c; Table 6).

There was an indication of a negative association between the level of urbanisation and the number of chicks fledged in Great Tits ($p = 0.05$; Fig. 6d), but the null model was within $\Delta 2$ AICc of that minimal model, indicating low model support. While only nests in which one or more chicks successfully fledged were studied, no evidence of an effect of arthropod or ectoparasite numbers, nest construction or level of urbanisation on the number of chicks fledged was found.

Fig. 2 The influence of the proportion of green surfaces (natural surfaces and gardens) on nest arthropod Shannon diversity index. Plotted line of best fit (with 95% confidence intervals) is based on predictions extracted from the linear mixed-effect model with Shannon diversity as the dependent variable. Site and nest box were random factors. The broad habitat types around the nest boxes are indicated

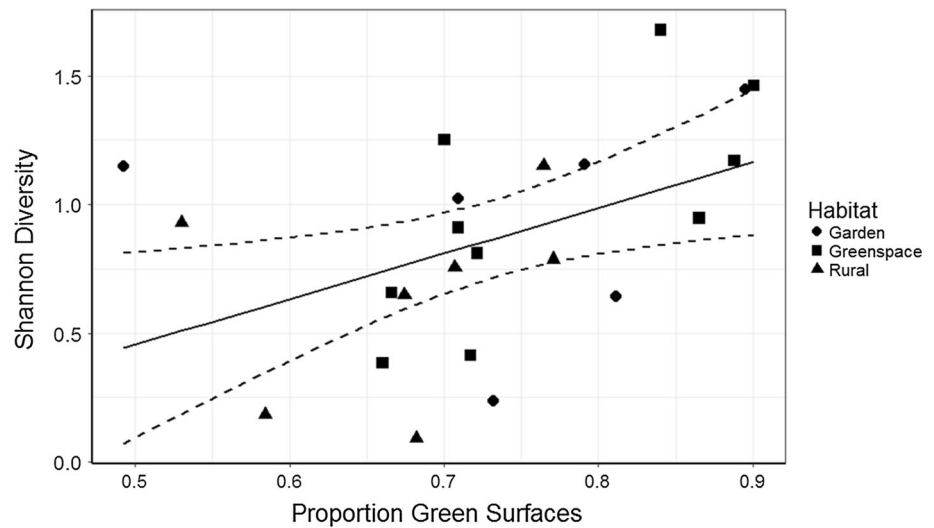


Table 4 Summary of linear mixed-model effect factors on Shannon diversity of arthropods in Blue Tit nests

Model	Covariates	Estimate	SE	df	χ^2	p	Δ AICc	Model weight
Null	Intercept only	0.8648	0.0831	NA	NA	NA	2.38	0.106
Global	Anthropogenic material	-0.5346	0.5123	4	7.81	0.0988	8.77	0.004
	Green surfaces	1.926	0.7368					
	Chicks fledged	-0.0083	0.0376					
	Nest dry weight	0.0074	0.0071					
Model 2	Green surfaces	1.670	0.7074	2	6.71	0.0349	1.93	0.132
	Nest dry weight	0.0085	0.0071					
Minimal	Green surfaces	1.773	0.7235	1	5.34	0.0209	0.00	0.347

ANOVAs were carried out between candidate models and the null model to determine model significance
 Δ AIC Delta Akaike information criteria, NA not applicable

Fig. 3 The influence of the proportion of anthropogenic nest material on the abundance of predators (total abundance of Pseudoscorpionida, Staphylinidae and Histeridae) living in Blue Tit nests, fitted with a linear line of best fit. The broad habitat types around the nest boxes are indicated

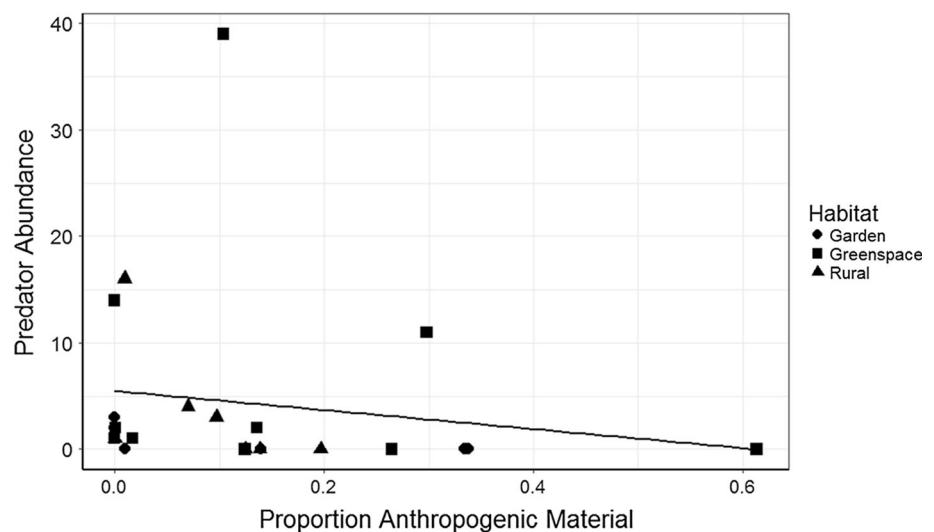


Fig. 4 The influence of **a** the proportion of constructed surfaces within 200 m of the nest box, and **b** the proportion of anthropogenic material comprising nests on overall flea abundance in fledged Great Tit nests. *Plotted lines* of best fit (with 95% confidence intervals) were based on predictions extracted from the respective mixed-effect model for these variables. Site and nest box were random factors. Broad habitat types around the nest boxes are indicated

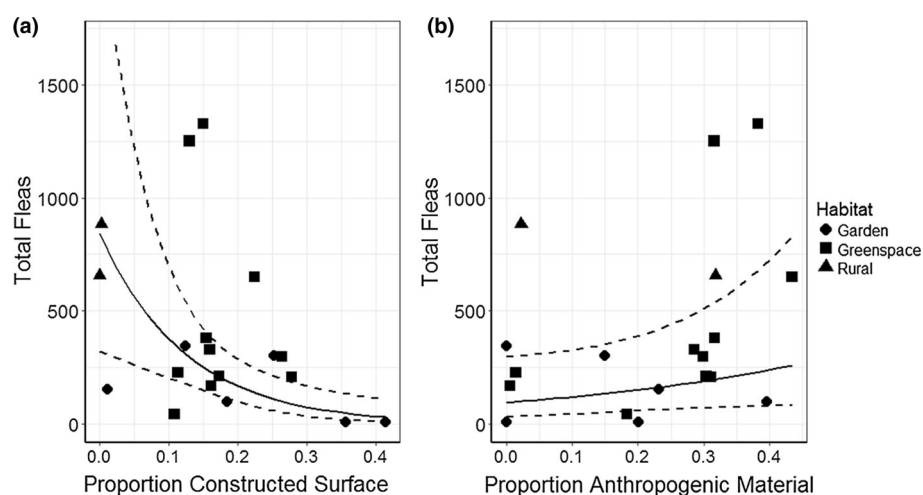
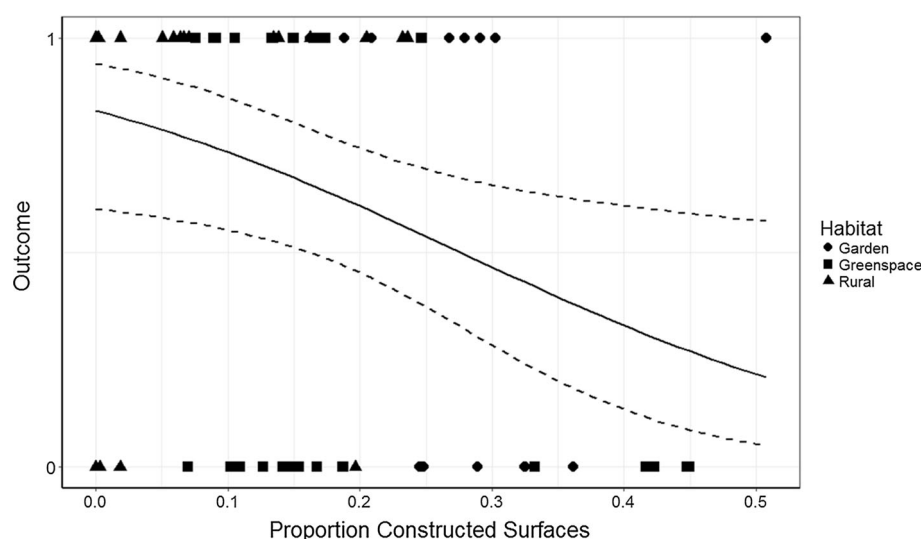


Table 5 Summary of Poisson mixed-model effect factors on flea (Siphonaptera) abundance in fledged Great Tit nests with $\Delta AICc$ and model weights

Model	Covariates	Estimate	SE	<i>p</i>	$\Delta AICc$	Model weight
Null	Intercept only	5.059	0.5128	<0.0001***	3.40	0.047
Global	Anthropogenic material	3.557	1.845	0.0539 [†]	14.1	0.000
	Constructed surfaces	−8.867	2.279	<0.0001***		
	Chicks fledged	−0.1754	0.1715	0.3065		
	Shannon diversity	−0.2375	0.6959	0.7330		
	Nest dry weight	−0.0076	0.0273	0.7806		
Model 2	Anthropogenic material	3.233	1.666	0.0523 [†]	0.32	0.219
	Constructed surfaces	−8.117	2.261	0.0003***		
Minimal	Constructed surfaces	−8.094	2.471	0.0011**	0.00	0.257

[†] $p = 0.1-0.05$, ** $p < 0.001$, *** $p < 0.0001$

Fig. 5 The influence of the proportion of constructed surfaces within 200 m of the nest box on the outcome of Blue Tit breeding success, where 1 indicates fledging at least one chick and 0 indicates failure. The *plotted line* of best fit (with 95% confidence intervals) was based on predictions extracted from the binomial mixed-effect model for nest outcome. Site and nest box were random factors. Broad habitat types around the nest boxes are indicated. Nests that failed through predation were excluded from this model



Discussion

Our work supports the view that increased urbanisation is generally associated with a reduction in the overall breeding success of wild birds (reviewed in Chamberlain

et al. 2009). We were surprised to find that while Great Tits and Blue Tits differed in their use of anthropogenic materials to construct nests (Great Tit > Blue Tit), this was not associated with urbanisation, suggesting perhaps an element of choice in nesting materials beyond simply their

Fig. 6 The influence of dry nest weight on **a** the number of eggs laid, and **b** the number of chicks fledged by Blue Tits. The influence of the proportion of constructed surfaces within 200 m of the nest box on the number of chicks fledged by **c** Blue Tits and **d** Great Tits. The plotted lines of best fit (with 95% confidence intervals) were based on predictions extracted from the respective mixed-effect model for these variables. Site and nest box were random factors. Broad habitat types around the nest boxes are indicated. Predated nests were excluded from the models considering the number of chicks fledged

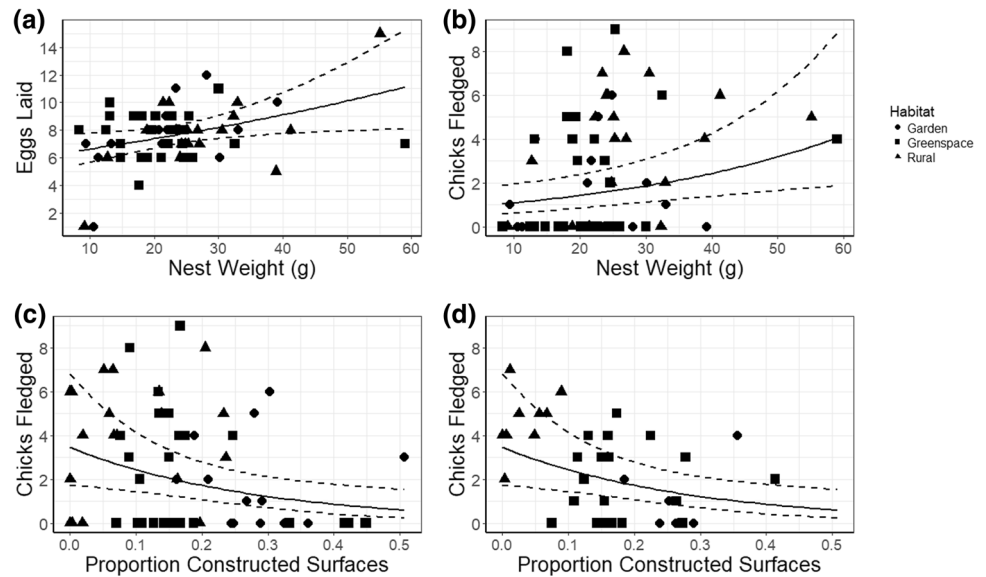


Table 6 Summary of mixed-model effect factors on the productivity of Blue Tit nests with ΔAICc and model weights

Dependent variable	Model	Covariates	Estimate	SE	<i>p</i>	ΔAICc	Model weight
Binomial outcome (failed/fledged)	Null	Intercept only	0.4761	0.3623	0.1890	4.70	0.038
	Global	Nest dry weight	0.07704	0.04787	0.1075	1.95	0.152
		Anthropogenic material	-1.196	1.807	0.5083		
		Constructed surfaces	-5.942	2.783	0.0327*		
	Model 1	Constructed surfaces	-5.750	2.502	0.0215*	1.61	0.180
	Minimal	Nest dry weight	0.07245	0.04491	0.1067	0.00	0.402
Eggs	Global	Constructed surfaces	-6.151	2.677	0.0216*		
		Intercept only	2.040	0.04579	<0.0001***	2.99	0.092
		Nest dry weight	0.01059	0.004556	0.0201*	3.75	0.063
	Model 1	Anthropogenic material	0.07996	0.2324	0.7308		
		Constructed surfaces	0.3131	0.3721	0.4000		
		Nest dry weight	0.01039	0.004514	0.0213*	1.50	0.194
Chicks fledged	Minimal	Constructed surfaces	0.3282	0.3687	0.3734		
		Nest dry weight	0.01054	0.004514	0.0195*	0.00	0.411
		Intercept only	0.5148	0.2615	0.0490*	11.57	0.002
	Global	Number of eggs laid	0.009600	0.04553	0.8330	4.54	0.049
		Nest dry weight	0.02337	0.01073	0.0295*		
		Constructed surfaces	-3.708	1.275	0.0036**		
	Minimal	Anthropogenic material	-0.3484	0.6426	0.5877		
		Nest dry weight	0.02538	0.009564	0.0080**	0.00	0.478
		Constructed surfaces	-3.791	1.251	0.0024**		

For the binomial outcome and chicks fledged models, nests that failed through predation were excluded

* $p < 0.01$, ** $p < 0.001$, *** $p < 0.0001$

availability. There was no difference in nest mass among habitats for Great Tits, but Blue Tit nests in rural areas were significantly heavier, and overall, heavier nests were associated with greater fledging rates. Both bird ectoparasites and nest-dwelling arthropods more generally showed

evidence of declining with increasing loss of green space. However, there was a negative correlation between flea load and overall arthropod diversity in nests, suggesting that arthropods may have been preying on flea larvae and/or eggs, or acting as competitors for resources. At the same

time, while overall arthropod diversity and predator numbers were both negatively associated with increased proportional use of anthropogenic nesting material in nests, flea numbers conversely increased. We speculate that the reduction in the use of natural nesting materials reduces overall diversity in the arthropod nest box assemblage, which in turn reduces the effects of predation and/or competition on flea abundance.

Understanding of the role of nests has increased considerably in recent years, but the nest-building phase of breeding success is relatively understudied (Deeming and Reynolds 2015). Nests represent a major energy investment (Mainwaring and Hartley 2013) and understanding their role, particularly in the light of urbanisation, may help us to understand changes in productivity across habitat gradients and their conservation implications. In addition to finding a broad decline in reproductive output associated with urbanisation, as found elsewhere (Chace and Walsh 2006; Chamberlain et al. 2009), we also similarly found heavier nests to be linked with higher reproductive output. This concurs with a number of previous nest box studies, though not all (Lambrechts et al. 2016b), and may be linked to adult quality (Alvarez et al. 2013; Gladalski et al. 2016; Lambrechts et al. 2016a). Such differences in turn may be linked to differences in nesting behaviour and reproductive output between these species, as Blue Tits typically build proportionally heavier nests and have a higher average reproductive output per breeding attempt than the larger Great Tit (Lambrechts et al. 2014, 2015; Gladalski et al. 2016).

While the majority of nesting materials are intended to provide insulation and structure, nest components may also provide additional benefits. Aromatic plants may offer an anti-ectoparasite or even anti-bacterial function in nests (Mennerat et al. 2009a; Tomás et al. 2012; Ruiz-Castellano et al. 2016). Fewer native aromatic plants may be available at higher levels of urbanisation even though the overall plant diversity can be higher due to the planting of exotic plant species in gardens and other areas (McKinney 2008). The prevalence and importance of aromatic plants in the nests of breeding Blue Tits and Great Tits in the UK is unknown. However, Blue Tits have been found to utilise them elsewhere in their range (Mennerat et al. 2009a, b; Tomás et al. 2012). Artificial nesting materials do not offer defences against macro- or micro-parasites, and so their benefits are in terms of nest structure and insulation. Furthermore, as processed anthropogenic materials are largely artificial in origin, they will also not provide food resources for consumers (principally arthropods) and decomposers (mainly bacteria and fungi), and hence may affect the complexity of the structure of the assemblage of species (including predatory species) that inhabit the nest boxes.

We found variation in the use of anthropogenic nest components similar to that found in other studies on Blue

Tit and related species here in the UK and in Europe more generally (Moreno et al. 2009; Britt and Deeming 2011; Reynolds et al. 2016) although this variation is understudied (Deeming and Mainwaring 2015). Like Reynolds et al. (2016) we found that anthropogenic material was present throughout the site types and in the majority of nests irrespective of the local level of urbanisation. Great Tit nests contained a median of 24% anthropogenic material and this varied little across habitats, suggesting that they may preferentially seek these materials when nest building, particularly when they are uncommon (Surgey et al. 2012). This may be due to a preference for the materials' insulation properties and thus fitness benefits (Reynolds et al. 2016). In contrast, Blue Tit nests contained an overall median of 2% anthropogenic material, and while not statistically significant due to considerable variation among nests, we note that this increased to 16% in urban gardens, suggesting that Blue Tits are more opportunistic in their use of non-natural materials. This may be due to the decline of natural nesting material availability or an increase in the general availability of artificial substitutes in urban areas (Wang et al. 2009).

In contrast to Reynolds et al. (2016), we do find a possible effect of anthropogenic materials on the presence of ectoparasites and other arthropods. In Blue Tits a higher proportion of anthropogenic nest material is associated with lower arthropod diversity. While the majority of non-parasitic arthropods appeared to be opportunistic in nature, their numbers also included potential predators of flea larvae and eggs. These also appeared to decline with increasing use of anthropogenic materials. While a relationship between predator and flea numbers was not found, increased arthropod diversity was correlated with a decline in flea numbers. This may be a result of competition for resources [the consumption of adult flea frass which would otherwise be consumed by flea larvae (Tripet and Richner 1999), in a manner analogous to that found by Křištofík et al. (2017)] or predation of flea eggs and larvae.

Such changes in the degree of interspecific interactions may provide a functional explanation of the increase in flea numbers associated with an increase in the proportion of anthropogenic materials used in nests. We suggest that nests constructed with more natural materials support a more structurally diverse arthropod community (including more predators) and that this should reduce flea numbers irrespective of the level of urbanisation. Given this, it would be logical to expect birds to prefer natural materials where available. This makes the possible preference for anthropogenic materials shown by Great Tits unexpected if they are less exposed to them and more energy is expended in finding these materials (Surgey et al. 2012). As they appeared to seek these materials out regardless of overall

availability in the local environment, we speculate that they may derive other advantages from utilising them.

Such a relationship between anthropogenic materials and parasite load, even if indirect, may help explain findings by others on variation in nest ectoparasite loads with different materials (Moreno et al. 2009; Tomás et al. 2012; Cantarero et al. 2013; Reynolds et al. 2016). Nevertheless, it is not clear if nest material choice and associated changes in arthropod assemblage help explain variation in breeding success associated with urbanisation. This may simply be due to food availability being the most important factor driving the reduction in fledgling success seen in urban areas (Chace and Walsh 2006; Chamberlain et al. 2009) or that the effects of parasites are frequently hidden until nestlings become highly stressed (Simon et al. 2004; Arriero et al. 2008; Bañbura et al. 2011).

We acknowledge that our sampling approach was constrained; as nests could not be removed until after fledging we cannot be certain that the biodiversity recorded in removed nests represents that present in nests when they were being used [although previous work suggests the loss of fleas should have been low (Wesołowski and Stańska 2001)]. Furthermore, Tullgren funnels may not be the most effective way of sampling adult flea abundance (Harper et al. 1992; Moreno et al. 2009), which may explain the comparatively low numbers of adult fleas found in this study compared to others that used freezing and manual deconstruction of nests to find them (Reynolds et al. 2016). Nevertheless, the counting of flea larvae does provide a measure of nest flea abundance in the absence of adults, and this approach did allow us to collect the other nest arthropods present, which for species such as mites would have been very challenging to sample using other approaches (Moreno et al. 2009).

Cavity nesters that take easily to artificial nests sites provide an important research tool for exploring the effects of various factors on breeding success (Vaugoyeau et al. 2016), but it is important to bear in mind that nest box-based studies may not be directly comparable to those on nests in natural cavities (Wesołowski and Stańska 2001; Maziarsz et al. 2017). Nevertheless, in urban areas nest boxes may be the main nesting cavities available to Great and Blue Tits (Davies et al. 2009). Given the different responses detected in this study and by others of these two related species, it is important to consider that different bird species may respond differently to similar pressures (Lambrechts et al. 2015; Gladalski et al. 2016), so we must be mindful of drawing broad conclusions from single-species studies (Reynolds et al. 2016; Vaugoyeau et al. 2016). Due to the relatively poor breeding season during our fieldwork, sample numbers were lower than anticipated, which reduced the statistical power of our study. A larger/multiple year study also considering the reasons for nest failure would allow for a more

considered reflection on how these factors interact to affect the breeding success of urban birds.

Being an urban adapter brings novel opportunities [e.g. supplementary food (Orros and Fellowes 2015b; Hanmer et al. 2017, in review)] and challenges [e.g. domestic cats (Thomas et al. 2014, Hanmer et al., in review)]. Nest boxes provide a clear opportunity to birds when breeding sites are limited, but it is evident that increased urbanisation is associated with a decrease in the number of offspring successfully fledged in species which use nest boxes such as Blue and Great Tits (Cowie and Hinsley 1987; Chamberlain et al. 2009; this study). We examined how potential variation in nest construction may contribute to this reduction in breeding success, both directly (nesting materials affecting successful breeding) or indirectly (nests and nest boxes as homes to ectoparasites and other arthropods). Blue Tit nests in less urbanised areas tended to be heavier, with heavier nests leading to more eggs being laid and more chicks fledged, whereas no effect of urbanisation on nest weight was found in Great Tits. We found that Blue and Great Tits differ in how they utilise anthropogenic materials, with Great Tits showing higher rates of use, but no effect of urbanisation, whereas Blue Tits show some evidence of increased use in urban gardens where such material is likely to be more common. We found no evidence that the use of anthropogenic materials directly affected breeding success. However, while arthropod diversity and predator numbers declined with increasing use of anthropogenic nest materials, the number of fleas increased, suggesting that there may be indirect links between the materials used in nest construction and parasite (flea) load. Nest boxes are clearly ecological communities in their own right; we suggest that these may be more complex than they first appear, and worthy of consideration for further investigation.

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